PREDATION BY SPIDERS ON GROUND-RELEASED SCREWWORM FLIES, COCHLIOMYIA HOMINIVORAX (DIPTERA: CALLIPHORIDAE) IN A MOUNTAINOUS AREA OF SOUTHERN MEXICO¹

John B. Welch²: Screwworm Research, Agricultural Research Service, United States Department of Agriculture, Tuxtla Gutierrez, Chiapas, Mexico

ABSTRACT. Predation by spiders on ground-released adult screwworms, *Cochliomyia hominivorax* (Coquerel), was studied near Tuxtla Gutierrez, Chiapas, Mexico, during 13 August 1984–23 January 1985. Observations of predatory behavior and manual collections of spiders during September provided the majority of the data. Species in 12 genera of spiders were confirmed as predators of screwworm flies. *Nephila clavipes, Eriophora ravilla, Neoscona oaxacensis* and *Leucauge* spp. were the most important predators. Spiders caused an estimated 4.5% mortality to flies in a 2250 m³ area during September. Capture of screwworm flies in webs up to 10 m above ground suggests the need to investigate the importance of forest canopies in screwworm ecology.

The screwworm fly, *Cochliomyia hominivorax* (Coquerel), native to the western hemisphere, is an obligate parasite of warmblooded animals. Studies of the ecology of screwworms in the tropics have been conducted since the late 1970's (e.g., Krafsur et al. 1979; Spencer et al. 1981; Brenner 1985; Mangan & Thomas 1989). However, information on predation of screwworms is generally lacking.

My interest in predation of screwworms began during an unpublished study of dispersal of ground-released adult screwworm flies in a mountainous area of southern Mexico. On the occasions of the first two releases of flies (22 May and 6 July 1984), spider populations were apparently low because few spiders and webs were seen during the collection of the fly samples. Numerous spiders and webs were encountered during trips to the study area the week before the planned third release (14 August). Spiders continued to be numerous prior to the fourth release (25 September). Spider populations appeared to decline after this release, as few spiders and webs were observed while collecting fly samples during the fifth and sixth releases (13 November 1984 and 22 January 1985).

The results of an investigation into predation

on adult screwworm flies during the third and fourth releases are presented herein. Additional data concerning spider predation during the fifth and sixth releases and other screwworm fly dispersal studies are included. Information on the predatory behavior of spiders is also presented.

METHODS

The study was conducted in the Sumidero Canyon National Park located *ca.* 15 km north of Tuxtla Gutierrez, Chiapas, Mexico. Spiders were also collected from Finca San Rafael, a study site *ca.* 32 km south of Tuxtla Gutierrez during another trapping study of *C. hominivorax* (Welch 1988).

The study site in the Sumidero Canyon National Park was located on the southern face of the mountain at an elevation of *ca.* 1040 m above mean sea level. The habitat was a low deciduous forest (Miranda 1975) comprised predominantly of trees *ca.* 3–8 m tall, with scattered, emergent trees above the canopy. The study site at Finca San Rafael was also situated in a low deciduous forest, although the trees were taller (ca. 4–10 m) and the vegetation was more dense.

Sterile screwworm pupae of the A-82 strain obtained from the sterile-fly production plant of the Joint Mexico-U. S. Commission for the Eradication of Screwworms were placed in the field on 25 September (and the other release dates) and allowed to emerge. Pupae were marked with 20 g/liter of fluorescent powder (Dayglo Color, Cleveland, Ohio) and distributed in open card-

¹ Mention of a proprietary product does not imply an endorsement or a recommendation for its use by USDA. ² Current address: USDA-ARS Screwworm Research, Center for Space Research, WRW 402, The University of Texas at Austin, Austin, Texas 78712–1085 USA

board cartons $(1.45 \times 18 \times 4 \text{ cm}; 0.5 \text{ liter/car$ $ton})$ stacked inside a wooden crate $(26.5 \times 36 \times 49.5 \text{ cm})$. The crate was covered with a corrugated tar-paper roof for protection and suspended 1.5 m above ground by wire from a tree limb. This is termed "ground-released" as opposed to being released from an airplane. Percentage of emergence was determined from controls (0.5 liter carton of marked pupae enclosed within a screen bag inside the release crate) (Welch 1988). All flies were examined under longwave ultraviolet light for fluorescent markings on the frontal suture (Brenner 1984).

Predation data were obtained by direct observation and by collection of spider and fly samples. Spider and fly activities were monitored visually at the Sumidero release site 5 from 0630 to 1600 h (time period due to park hours) on 26 and 27 September. Three pitfall traps filled with 70% ethyl alcohol were operated from 25-29 September, 13-17 November, and 22-26 January. Fly emergence ended and manual collections of spiders and sweep samples of the vegetation in the vicinity of release site 5 were conducted on 28 September. Spiders with screwworm flies in their webs were also collected from other release and trap sites within the Sumidero Canyon National Park and Finca San Rafael throughout the remainder of the study period.

A search for screwworm fly cadavers and spiders was made along a transect (150 m) heading south of release site 5 on 28 September. The transect was located along an existing trail descending the mountain because cutting of new trails or paths within the park was prohibited.

Specimens were sent to William B. Peck for identification. Voucher specimens are maintained in a collection at the United States Department of Agriculture, Agricultural Research Service, Screwworm Research Laboratory at El Alto de Ochomogo near San Jose, Costa Rica (as is typical in Costa Rica, the actual laboratory site has no street or mailing address; requests for information concerning the voucher specimens should be directed to the author at his listed mailing address).

RESULTS

A total of 126 spiders representing 12 families and ca. 26 species were collected during this study. Most (78.6%) of the spiders belonged to the families Tetragnathidae and Araneidae, with Nephila clavipes L., Leucauge spp., Neoscona oaxacensis (Keyserling) and Eriophora ravilla (C. L. Koch) accounting for 19.0, 19.0, 14.3, and 13.5% of the total spiders collected, respectively. Other araneid genera included *Micrathena*, *Verrucosa*, and *Mangora*. Spiders belonging to the families Filistatidae, Tengellidae (*Zorocrates*), Plectreuridae (*Plectreurys*), Theridiidae (*Argyrodes*), Lycosidae (*Lycosa*), Oxyopidae (*Peucetia*), Clubionidae, Sparassidae, Selenopidae (*Selenops*), Thomisidae (*Misumenoides*, *Misumenops*) and Salticidae (*Phidippus*) were also collected. The majority (103 specimens, 7 families) of the spiders collected were captured manually, while 5 specimens representing 4 families were collected by pitfall trap, and 18 specimens representing 3 families were collected by sweep sample.

Predation by spiders on screwworms was evidenced by dead flies in the webs of spiders (Table 1) and by direct observation of flies being captured. Species of Misumenops sp. and Misumenoides sp. were collected, each with one screwworm fly. Additionally, a Peucetia viridans (Hentz) was discovered with two dead flies on one occasion. Species of 11 genera of spiders captured screwworm flies in webs during the study. The four most commonly collected groups of spiders listed above also accounted for the most (91.5%) webs containing screwworm flies (Table 1). Webs of N. clavipes accounted for 43.9% of those with ensnared flies. Eriophora ravilla, N. oaxacensis, and Leucauge spp. webs accounted for 19.0, 17.8 and 9.5%, respectively, of the webs with flies. All webs of N. clavipes and 88.9 and 93.7% of webs of E. ravilla and N. oaxacensis, respectively, contained screwworm fly cadavers. Only 40.0% of the webs of Leucauge spp. contained dead flies.

A rough estimate of percent predation of screwworms may be obtained from the collections of data along the transect heading south of the release crate at release site 5. A total of 389 screwworm flies were observed in webs along the transect within 75 m of the release crate. Webs were located within ca. 3 m of the transect and up to 10 m above the ground. Based on emergence of controls, an estimated 8710 flies were released from the site, thus resulting in a calculation of 4.5% mortality of flies by spiders within the 2250 m³ area of the transect. Inspection of the surrounding area resulted in few additional webs being located and no screwworms were seen in the webs. Therefore, the estimate would only be valid for the area of the transect; and it is still imprecise because flies killed and removed from the webs, and flies that were bitten and escaped

from the web, but then died, etc. were not counted.

Although not along the transect, a fly released from site 1 got caught in a web of N. oaxacensis located 150 m to the south, the record distance between release site and point of entanglement in a spider web during this study.

Due to the small sample size, fly capture data were pooled for all spider species. Generally, more flies per web were ensnared from 1-10 m from the release crate than from 11-20 + m for most species of spiders (Fig. 1). Most webs of all species (64.6%) along the transect were 1-3 m above ground and accounted for the most screwworm flies ensnared. More webs (27.7%) were 7-10 m than 3.5–6.5 m above ground (7.7%), and more flies were caught in the higher webs than those located within the 3.5-6.5 m range (Fig. 2). This pattern was exhibited by N. clavipes and E. ravilla webs. Entanglement in webs of Neoscona oaxacensis occurred 1-3 m above ground, and the webs of the unidentified species were mostly 1-3 m above ground.

Observations of fly activity at the release site indicated that flies began leaving the release crate at 0800 h on 26 September and continued until observations were stopped at 1600 h. Fly activity began at 0637 h on 27 September and continued until 1437 h, at which time dispersal from the release crate was complete. On both days, fly activity increased when direct sunlight reached the release crate, and slowly decreased when direct sunlight was blocked by clouds. No flies left the release crate while it rained, and flies outside of the release crate moved to the undersides of leaves and rocks during the rain.

Observations on the predatory activity of spiders in webs within three m of the release crate were made in relation to screwworm flies emerging from the release crate at release site 5. Individuals of N. clavipes (five females) began feeding on the flies immediately as the flies became trapped in the webs on the morning of 26 September. This activity continued from 0800 h until ca. 1020 h, when the spiders began repairing the webs. Predation and web repair continued throughout the afternoon while the flies were active. However, spiders began ignoring some of the new flies caught in the webs ca. midday (e.g., one spider with 29 flies in its web began ignoring the flies at 1148 h and another spider with 14 flies in its web began ignoring other flies at 1151 h). Flies that were ignored and not killed immediately had time to make a possible escape.

Table 1.—Species of spiders and number of webs containing at least one cadaver of *Cochliomyia hom-inivorax* after field release. Cadavers also were found in the webs of an unidentified theridiid and other unidentified species.

Species	Number of webs	
	With prey	Without prey
Plectreurys sp.	1	0
Argyrodes sp.	1	3
Araneus sp.	1	0
Eriophora ravilla	16	2
Nephila clavipes	36	0
Micrathena spp.	2	2
Verrucosa arenata	2	0
Neoscona oaxacensis	15	1
Leucauge spp.	8	12
Total	82	20

Approximately 27.5% (19 of the 69) of the flies caught in the webs of N. *clavipes* escaped during the study period on 26 September.

At 1420 h, a female *E. ravilla* climbed onto a web of a female *N. clavipes*, and the *N. clavipes* rapidly retreated to the vegetation to which the web was anchored. The *E. ravilla* began examining the dead flies (11) in the web and initiated repairs to the web. After repairs were completed, the spider began preying on newly captured flies and maintained the web for the remainder of the afternoon. Upon my arrival at the study site on the morning of 27 September, the female *E. ravilla* had vacated the web, and what appeared to be the original *N. clavipes* owner (based on size and appearance) had returned and was repairing the web. This specimen continued predation in the web and the *E. ravilla* did not return.

The web of the largest female *N. clavipes* had not been repaired by the morning of 27 September, had several large holes and was cluttered with the corpses of flies. This individual made no attempt to repair the web and did not react to any new flies hitting her web during the day. All of the flies that were caught in her web on 27 September escaped.

The percentage of flies escaping the webs of N. clavipes on 27 September could not be estimated because the numbers of flies that were hitting the webs and escaping were too numerous to count. At one point during the morning (0745 h), during peak dispersal of the flies, it was estimated that ca. 40 flies per minute were hitting the webs.

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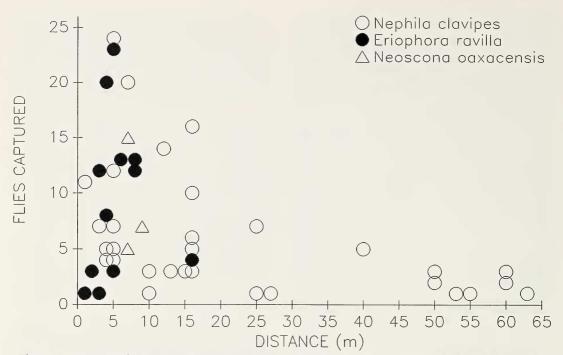


Figure 1.—Number of screwworm fly cadavers found in webs of three species of spiders located from 1-75 m from the release box.

Nineteen screwworm flies were observed being preyed upon during the hours of 0655-1130 by *N. clavipes.*

Observations on the predation activity of eight female *E. ravilla* were made in relation to the release crate at release site 5. Predation activity of *E. ravilla* also began on the morning of 26 September when the dispersing screwworm flies began hitting the webs. At first, webs were repaired immediately after the flies were killed and removed. However, beginning around 1020 h, the spiders ceased repairing the webs. Then at 1108 h some individuals of this species began ignoring live flies entangled in their webs. Flies were ensnared and killed throughout the day until observations were stopped at 1600 h.

A total of 88 screwworm flies was ensnared in webs of E. ravilla on 26 September. Seventeen flies escaped from the webs, resulting in an estimated 19.3% escape.

Although more flies were dispersing on 27 September, *E. ravilla* began ignoring the flies hitting the webs after 0848 h. Three of seven screwworm flies ensnared before 0848 h escaped, resulting in an estimated 42.9% escape for that time period.

Predation of screwworm flies dispersing from

the release crate at release site 5 by three female N. oaxacensis showed the same pattern as that by N. clavipes and E. ravilla. Predation on 26 September began immediately when the flies began hitting the webs and continued until 1530 h. Flies began escaping from the webs at 1035 h with an overall 12.7% escape (7 of 55). Spiders also began repairing their webs around 1020 h.

Most of the flies caught in the webs of N. oaxacensis on 26 September had been removed by 0630 h on 27 September. Ensnarement of flies on 27 September began at 0654 h and continued until 1000 h. Two flies escaped during that time period, resulting in 11.8% escape.

DISCUSSION

Predation of screwworm flies by species of 12 genera of spiders was observed in this study. Specimens of E. ravilla, N. clavipes, N. oaxaccensis, V. arenata and P. viridans were the only spiders within these genera identified to species, with the first three being the most important predators.

Nephila clavipes apparently build their webs in areas within the forests which are probable flight paths of insects (Robinson & Mirick 1971). Collections of flies in webs up to 10 m above the

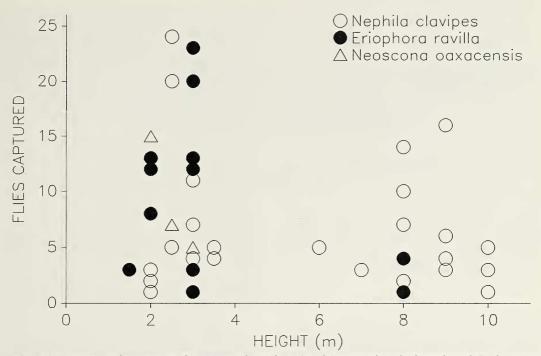


Figure 2.—Number of screwworm fly cadavers found in webs of three species of spiders from 0.5–10 m above the ground.

ground, in the area of the forest canopy, suggest that the forest canopy may be important to the ecology of screwworms. More screwworm flies have been collected in forest habitats than in pastures (Mangan & Thomas 1989). Studies of screwworms have been confined to ground level, so further investigations of the vertical distribution of screwworms in relation to habitat are needed.

The predatory behavior exhibited by the N. clavipes under observation agrees with the descriptions in the literature with one major difference. It was reported that N. clavipes always transported its prey to the hub of the web after immobilization (Robinson et al. 1969; Robinson & Mirick 1971). None of the five female N. clavipes that were monitored at release site 5 in my study exhibited this behavior: flies were never moved from the site of capture. Initially, when prey numbers were low, an immobilization bite was given and wrapping occurred at the capture site followed by apparent feeding on the prey in situ. When large numbers of flies were hitting the webs or when the spiders apparently became satiated, post-immobilization wrapping was omitted. The latter is in agreement with Robinson et al. (1969) and Robinson & Mirick (1971). This apparent feeding may have been what was referred to as a "long bite" by Robinson & Mirick (1971); however, because considerable time was spent by the spiders with the prey and later prey were ignored (suggesting the spiders' hunger was satiated), it appeared that the spiders were feeding. Upon my return to release site 5 on 27 September, corpses of flies were still present at the site of capture in the webs and none were present at the hub where the spiders were resting. Also, the bite and back-off behavior described by Robinson & Mirick (1971) was not exhibited by *N. clavipes* during my study, but this was probably due to the smaller size of the prey (i. e., flies *vs.* crickets) between the two studies.

Differences in percentages of prey escaping from *N. clavipes* webs between earlier studies and mine were probably due primarily to the unusually high density of screwworm flies in the area. An estimated 27.5% of the screwworm flies escaped from the webs on 26 September. Robinson et al. (1969) reported that 46% of the stingless bees (*Trigona* sp.) ensnared, escaped from the webs, primarily while *N. clavipes* was occupied at the hub of the web. However, no estimation was calculated for 27 September because too many flies to be counted were hitting the webs and were being ignored because the spiders were apparently satiated.

ACKNOWLEDGMENTS

The technical assistance of Eliseo Broca E., Alfredo Matias E., Carlos Moises E., Carlos Ojeda E. and Ramiro Penagos R. is greatly appreciated. Sterile flies used in this study were provided by the Joint Mexico-U. S. Commission for the Eradication of Screwworms. Permission to work in the Sumidero Canyon National Park was granted by Felipe Barbosa Rivera of the Secretaria de Desarrollo Urbano y Ecologia. I am especially grateful to William B. Peck for identification of spiders collected during this investigation. I also thank Frank D. Parker and David A. Dean for their reviews of an earlier version of this manuscript, and Matthew H. Greenstone, David Wise and an anonymous reviewer for suggesting changes incorporated in the revision.

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